Zoologisches Institut der Universität Basel, Schweiz

Spatial and seasonal distribution patterns of oribatid mites (Acari: Oribatei) in a forest soil ecosystem

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With 9 figures

Contents

1. Introduction

A study of dispersion, abundance and population dynamics of oribatid mites in a temperate mixed deciduous forest soil in north-west Switzerland was carried out from February 1979 to February 1980 (Schenker 1981). Based on this investigation, this paper reports on aspects of the distribution in space and time of the oribatid populations. The aims of this study were (1) — to describe oribatid distribution in relation to habitat structure and seasonal influences, (2) — to determine species composition and the influence of species distribution on abundance and biomass of the oribatid community, and (3) — to explain possible causes of the observed distribution patterns and seasonal changes in correlation with biotic and abiotic factors.

Several studies of oribatid distribution in different forest soils, e.g. aspen woodland (Mitchell 1978), beech wood (Luxton 1981), Scots pine (Usher 1975), as well as in other soils, e.g. meadows (Evison 1981) and moorland (Block 1966) have shown much variation in oribatid abundance in small areas and highly aggregated distribution patterns. This was demonstrated by Schenker & Streit (1981) for the area discussed here. Thus, for the present study, a well defined but diverse small-scale site was selected in order to make a more detailed field investigation of the oribatid dispersion patterns in a complex forest soil ecosystem.

2. Site description

The study area was located approximately 6 km south of Basel, Switzerland, on a plateau gently ascending towards the south. This region, the "Bruederholz" is used increasingly as a recreation area for people from Basel as it is relatively undisturbed and in close proximity to the city. The plateau is at ca. 390 m a.s.l. whereas the valley bottoms are at ca. 200 m a.s.l.

The study area was virtually a rectangle of 135 to 250 m (ca. 3.4 ha in area) on a 2°/₀ slope. It is delimited by meadows to the south and east, by enclosures of the "Brueder-
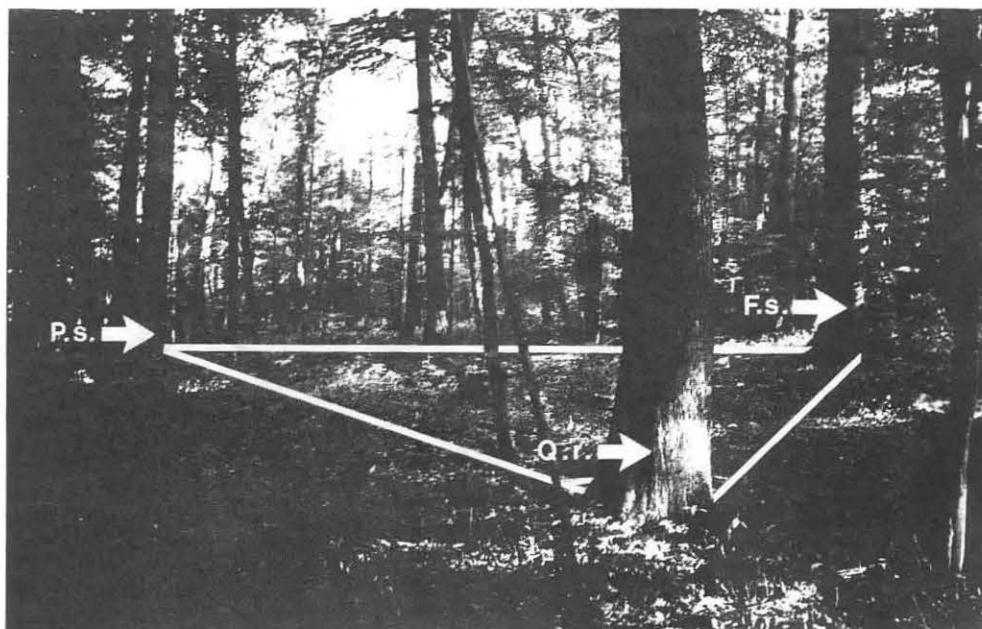
Fig. 1. Study site with the three tree species *Quercus robur (Q.r.)*, *Fagus silvatica (F.s.)* and *Pinus silvestris (P.s.)* characteristic of the forest.

holz" farm in the north whereas the forest is continuous to the west. It is a mixed deciduous forest of the Querco-carpinetum association with planted pine trees, the tree layer covering ca. 60%, of the area. The herb species are all moisture indicators (sub-association carice-tosum brizoides aretosum maculati) and several indicate wetness (*Prunus padus*, *De-schampsia caespitosa*, *Carex brizoides*, *Juncus conglomeratus*). However, where beech and pine trees occur in the tree layer the soil has a well developed structure with free drainage.

The site itself contained three tree species characteristic of the forest, i.e. *Quercus robur*, *Fagus silvatica* and *Pinus silvestris* standing in a triangle of ca. 12 m sidelength (Fig. 1). The tree species are referred to by their generic names hereafter.

The soil is a well drained brown-parabrown-earth on loess (Table 1). The humus layer showed a small-scale mosaic of mull and moder. Near *Quercus* moder humus was dominant, whereas near *Fagus* and *Pinus* mull humus was mainly found. The L-horizon was weak throughout the site and consisted of beech, oak and hornbeam litter as well as pine litter in varying proportions. The pH in the humus layer ranged from 3.8 to 5.2.

The climate is temperate with cool winters and long summers. The annual fluctuation of the monthly mean temperature ranges between 16 and 25 °C. Table 2 shows the long-term mean values for temperature, rainfall and relative humidity from 1931—1960 measured at the nearby meteorological observatory Basel-Binningen together with the means for the study year (1979-80) for comparison.

The temperature in the litter layer, measured at each sampling, ranged from 1.8 (Fe-bruary 1980) to 19.8 °C (August 1980), whilst in the soil (5 cm depth) it ranged from 3.5 to 19.8 °C in the same months. Soil moisture content varied from 17.2 to 28.4%, (wet mass) with its minimum in October and maximum in February 1980.

3. Methods

Monthly soil and litter samples were taken from February 1979 to February 1980. The soil sam-pler, a longitudinally divided iron tube, held PVC-cylinders (inner diameter 59 mm) which could be replaced by opening the tube distally. The soil sample remained in the PVC-cylinder, which was

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Table 1. Soil profile of a Loess-Brownearth-Parabrownearth at the study site

Loess-brownearth-parabrownearth

Site: gentle slope, gradient ca. 2%
Substrate: loess
Vegetation: oak-hornbeam forest
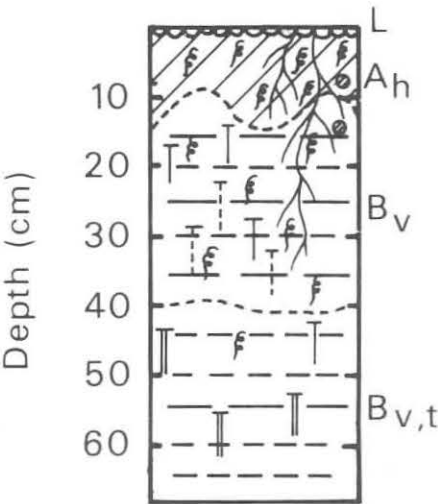
Profile description:

L.   Litter layer consisting of beech, oak and hornbeam leaves, some pine needles (1–2 cm).

A_h Darkbrown-grey (10 YR 3/2), extensive root system, porous, high worm activity, good decomposition of the organic material (0–8/15 cm).

B_v Medium brown (10 YR 4/4), moderate root system, high worm activity, porous (8/15–40 cm).

$B_{v,t}$ Light brown (10 YR 5/6), some of the material leached from the B_v-horizon partitioned here, weak root system (40 cm and deeper).

Physical and chemical soil parameters:

Depth in cm	Horizon	pH	Humus			Organic matter content (%)	Nutrients (ppm)		
			C (%)	N (%)	C/N		K	Ca	Na
5	A_h	4.4	4.1	0.29	14.0	8.0	2,463	1,413	6,210
10	A_h	4.0	1.4	0.18	7.7	4.4	1,642	631	4,830
15	A_h	3.8	1.2	0.17	7.0	3.3	1,349	120	5,060
20	B_v	3.9	0.9	0.13	7.2	2.8	1,173	150	5,520
30	B_v	3.9	0.8	0.11	7.6	2.3	1,056	180	5,290
40	$B_{v,t}$	<4.0	0.7	0.09	7.7	1.8	1,114	361	5,520
50	$B_{v,t}$	4.1	0.4	0.09	4.6	2.1	1,349	752	6,900

Signatures:

⌣⌣⌣⌣	Litter layer	↑	Oxidized
⌁⌁⌁	Horizon boundary	T	Leached clay
//////	Medium to high humus content	∏	Clay accumulation
— —	Silt	ℰ	Wormburrows
- - - - -	Clay	⅄ ∅	Roots

(Signatures after RICHARD et al. 1978)

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Table 2. Long-term mean values of temperature, precipitation and relative air humidity at Basel-Binningen (1931—1960, upper values) and comparative values for the study year (1979/80, lower values)

	J	F	M	A	M	J	J	A	S	O	N	D	
Air tempe-rature (°C)	0.1	1.3	5.4	9.3	13.5	17.0	18.7	18.0	14.8	9.4	4.8	1.2	9.4
	0.1	2.5	6.7	8.2	13.1	17.4	18.4	16.7	15.0	11.3	5.1	4.9	9.5
Precipitation (mm)	53	40	48	55	76	93	86	94	79	61	56	44	785
	60	85	55	54	61	93	56	145	39	60	69	55	842
Mean relative air humidity (%)	83	79	74	70	73	73	73	75	81	84	85	85	78
	83	86	74	67	67	74	64	75	77	85	83	78	76

closed at both ends with polyethylene caps for transportation and storage. Using up to four cylinders each of 5 cm height, a sampling depth of 20 cm was obtained. Samples were usually collected to a depth of 5 cm, corresponding approximately to the A_h-layer of the humus, but also to a depth of 20 cm divided into 5 cm subsamples.

Fig. 2 shows the distribution of the sampling points. Equally spaced samples were taken in concentric circles around each of the three trees and on straight transect lines between the trees. The sampling pattern changed in subsequent months (see Fig. 2), but was repeated every third month. The samples at a distance of 30 cm from the tree and to a depth of 5 cm were contained in all sampling distributions and thus collected every month. Therefore it was possible to use the results from these samples for a complete year and to obtain information, every third month, about the vertical distribution, the distribution pattern between and around (10—70 cm distance) the trees.

The soil arthropods were extracted in a modified high gradient Macfadyen extractor. It was designed to process 96 samples simultaneously. The temperature was controlled automatically and maintained constant above (26 °C) and below (ca. 19 °C) the samples. In efficiency tests more than 90% of the micro-arthropods were extracted (BIERI et al. 1978).
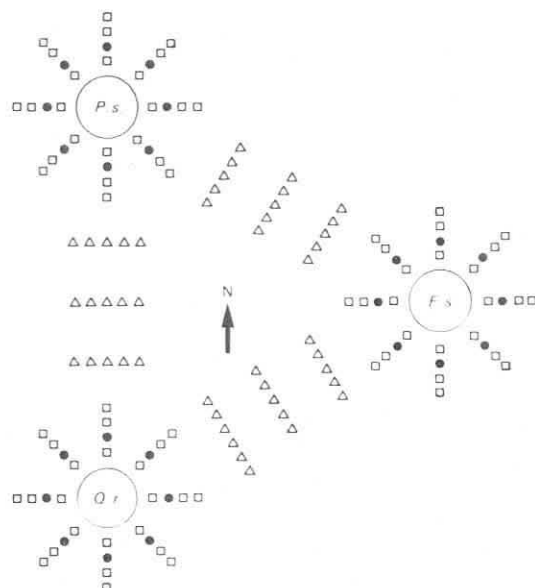

Fig. 2. Sample distribution and mode of sampling. Samples on concentric circles at 10, 30, 50 and 70 cm from the tree base. Samples on transects at 3, 6 and 9 m from the tree bases. ● and △ (69 cores) taken in February, March, June and December 1979. ● and ── (96 cores) taken in April, July, October 1979 and January 1980. ● (96 cores) 20 cm deep, divided into 5 cm sub-samples, taken in May, August, November 1979 and February 1980. All samples ● were part of each sampling mode and therefore taken monthly. *Q.r.: Quercus robur, F.s.: Fagus silvatica, P.s.: Pinus silvestris.* Distance between the trees ca. 12 m.

The animals were extracted into isopropanol and separated into groups (families or orders) and counted using a binocular microscope (120 ×). The oribatid species were identified and counted using a high power microscope.

Species diversity is expressed as the Shannon-Wiener index ($H = - \sum\limits_{i=1}^{s} (p_i)(\log_2 p_i)$, where H = index of species diversity, s = number of species, p_i = proportion of total sample belonging to ith species), and as Eveness $\left(E = \dfrac{H}{H_{max}} \right.$ where E = Equitability or Eveness, $H_{max} = \log_2 s \Big)$ which gives a diversity index independent of the number of species present.

The computer program used to plot the density maps was GEOMAP (Dept. Geography, Univ. Waterloo, Ont., Canada) available through the Computer Centre of the University of Basel.

Calculations of biomass are based on data given by different authors and summarized by LUXTON (1975). Where possible, data obtained by direct methods were used, i.e. weighing instead of calculation from measurements.

Soil moisture was determined gravimetrically from separate samples by the mass difference of 100 cm^3 fresh soil material after drying for 10 h at 105 °C. pH values were measured in the field with a HELLIGE "PeHa-Meter" and in the laboratory, the soil sample suspended in H_2O and KCl. Pore volume (PV) was calculated from the volume dry mass (V_t) and the specific mass (s) $\left(PV = 100 - \dfrac{V_t \cdot 100}{s} \right)$. The organic matter content was expressed as loss on ignition at 500 °C as a percentage of the dry mass. Carbon content was determined by acid oxidation. Carbon was oxidised with potassium dichromate and the freed Cr^{3+} ions were measured colorimetrically. The calibration curve was made with Na oxalate ($Na_2C_2O_4$). Nitrogen was determined after Kjeldahl with the "Büchi-nitrogen-determination-system" (Büchi 425/320). After disintegrating soil samples in ammonium lactate — acetic acid, the content of Ca, K and Na was determined in a flame photometer.

4. Results

4.1. Species composition and diversity

In the present study, 1,113 core samples were processed and 82,436 arthropods extracted. Of these, 28,587 were oribatid mites (34.7%). Only Collembola were present in greater numbers, i.e. 35,305 (42.8%), 31,904 being Arthropleona and 3,401 Symphypleona. A total of 65 oribatid species belonging to 37 genera were identified and are listed in Table 3.

Up to a distance of 70 cm from the trunks of the three trees, all but two species, *Amerus troisii* and *Carabodes femoralis*, were found. These taxa were rare and only occurred in samples collected between the trees. Around *Quercus* a total of 38 species (59%) of all species identified were recorded in the year of investigation, whilst around *Fagus* and *Pinus* 42 (65%) and 44 species (68%) respectively were recorded. 22 species (34%) were common in the area around all three tree species, whereas a few were found only around one of the trees, i.e. around *Quercus* 5 species (8%), around *Fagus* 8 species (12%) and around *Pinus* 11 species (17%). Around both *Quercus* and *Fagus* 6 species (9%) occurred, around *Fagus* and *Pinus* 6 species were found as well, whereas 5 species (8%) around *Quercus* and *Pinus*. In the inter-tree space 40 species (62%) were recorded.

Species diversity was highest around *Quercus* (annual mean from the samples taken at a distance of 30 cm from the trees), where H was 2.4 ($H_{max} = 4.4$) with a minimum in December ($H = 1.7$) and a maximum in May ($H = 2.9$). The Eveness was 0.5 for *Quercus* with a minimum in September ($E = 0.3$) and a maximum in February 1979 ($E = 0.8$). Around *Fagus* the mean annual diversity H was 3.2 ($H_{max} = 7.9$) the minimum being February 1979 ($H = 2.7$) and the maximum in March ($H = 3.8$) for the year. This corresponds to the mean Eveness of 0.4 (minimum in January: $E = 0.3$, maximum in February 1979: $E = 0.7$). *Pinus* with the greatest number of species showed the lowest diversity ($H = 2.0$, $H_{max} = 7.9$, minimum in March: $H = 1.3$, maximum in May: $H = 3.1$; $E = 0.3$, minimum in March: $E = 0.1$, maximum in May: $E = 0.4$). This was caused by the high abundance of a single species, *Tectocepheus velatus*, around this tree species (SCHENKER in press).

Vertically there was a sharp decline in species number from the 0—5 cm depth soil layer to the three deeper layers (5—10, 10—15 and 15—20 cm). Of the 38 species around *Quer-*

Table 3. Species list of all oribatid mites recorded at the study site. Recorded around: *Quercus, Fagus* and *Pinus* (1); *Quercus* (2); *Fagus* (3); *Pinus* (4); *Quercus* and *Fagus* (5); *Fagus* and *Pinus* (6); *Quercus* and *Pinus* (7); recorded on transect only (8); recorded around trees and on transect (+).

Species	Code
Palaeacarus hystricinus TRÄGÅRDH, 1932	1
Pilizetzia larvipalpus (C. L. KOCH, 1841)	1
Pilizetzia monogmus GRANDJEAN, 1963	1
Steganacarus magnus (NICOLET, 1855)	7
Steganacarus duliacus (OUDEMANS, 1906)	6
Brachychthonius berlesei WILLMANN, 1928	6
Brachychthonius italicus (BERLESE, 1910)	6
Brachychthonius zelawaensis SELLNICK, 1928	4
Brachychthonius annuradulus FORSSLUND, 1942	
Nothrus palustris C. L. KOCH, 1839	3
Nothrus silvestris NICOLET, 1855	3
Platynothrus peltifer (C. L. KOCH, 1839)	1
Malaconothrus globiger TRÄGÅRDH, 1910	6
Trimalaconothrus maius SELLNICK, 1921	3
Nanhermannia elegantula BERLESE, 1913	6
Liodes fuscosus (C. L. KOCH, 1840)	4
Platyliodes scaliger (C. L. KOCH, 1840)	4
Damaeus clavipes (HERMANN, 1804)	5
Damaeus gracilipes (OUDEMANS, 1929)	1
Cepheus explicatiformis (NICOLET, 1855)	7
Amerus troisii (BERLESE, 1883)	8
Eremaeus hepaticus C. L. KOCH, 1836	2
Adoristes ovatus (C. L. KOCH, 1840)	1
Liacarus coracinus (C. L. KOCH, 1840)	2
Liacarus tremellae (LINNÉ, 1761)	2
Xenillus tegeocranus (HERMANN, 1804)	3
Carabodella jucunda (MICHAEL, 1885)	3
Carabodes coriaceus C. L. KOCH, 1836	2
Carabodes minusculus BERLESE, 1923	1
Carabodes femoralis (NICOLET, 1855)	8
Carabodes marginatus (MICHAEL, 1884)	6
Odontocepheus elongatus (MICHAEL, 1879)	4
Tectocepheus velatus (MICHAEL, 1880)	1
Tectocepheus sarekensis (TRÄGÅRDH, 1910)	3
Oppiella translamellata (WILLMANN, 1923)	3
Oppiella obsoleta (PAOLI, 1908)	1
Oppiella fallax (PAOLI, 1908)	1
Oppiella minus (PAOLI, 1908)	1
Oppiella longilamellata (MICHAEL, 1885)	1
Oppiella quadricarinata (MICHAEL, 1885)	3
Oppiella nova (OUDEMANS, 1900)	3
Oppiella ornata (OUDEMANS, 1900)	4
Suctobelba trigona (MICHAEL, 1888)	1
Suctobelbella subtrigona (OUDEMANS, 1900)	1
Oribella castanea (HERMANN, 1804)	2
Cymbaeremaeus cymba (NICOLET, 1855)	4
Micreremus brevipes (MICHAEL, 1888)	5
Liebstadia humerata (SELLNICK, 1928)	1
Hemileius initialis (BERLESE, 1908)	5
Oribatula criits (NICOLET, 1855)	1
Oribatula tibialis (NICOLET, 1855)	1
Scheloribates pallidulus (C. L. KOCH, 1840)	1
Scheloribates confundatus SELLNICK, 1928	1
Scheloribates latipes (C. L. KOCH, 1844)	1
Scheloribates laevigatus (C. L. KOCH, 1836)	6
Trichoribates trimaculatus (C. L. KOCH, 1836)	6
Euphdops nuritus (C. L. KOCH, 1840)	1
Euphdops pinratus (C. L. KOCH, 1836)	1
Oribatella calcarata (C. L. KOCH, 1836)	7
Parachipteria reloptratus (LINNÉ, 1758)	3
Parachipteria punctatus (NICOLET, 1855)	4
Amerobelba sp.	4
Galumna aurabiaca OUDEMANS, 1914	4
Galumna areolata WILLMANN, 1932	2

cus, all from samples taken to a depth of 5 cm, only 9 species were found at 5–10 m depth and 4 species each in the 10–15 and 15–20 cm layers. Around *Fagus* the number of species decreased from 42 to 11, 7 and 10 species with increasing depth. For *Pinus* the corresponding values are 44 species in the uppermost layer and 9, 10 and 5 species in the subsequent lower layers.

Species diversity normally decreased with depth, but occasionally the reverse was the case as the remaining species occurred in a similar abundance. Higher diversity in the deeper layers compared to the upper 5 cm layer was for instance recorded around *Quercus* in November ($E_{0-5} = 0.8$, $E_{5-10} = 1.0$, $E_{10-15} = 0.9$, $E_{15-20} = 0.9$: SCHENKER 1981).

4.2. Spatial and seasonal distribution patterns

4.2.1. Horizontal distribution

In addition to the generally aggregated distribution of oribatid mites (BUTCHER et al. 1971), they were also unevenly distributed over the study site. Fig. 3 shows the abundance of oribatids around the three tree species at various distances from the trunk bases and at different seasons. Around *Quercus* the abundance was low, between 2 and 7 individuals per 130 cm³. Also, there was no significant difference between the abundance at various distances from the tree nor between different seasons.

The density of oribatids around *Fagus* was significantly higher than around *Quercus* and there was a clear density gradient with increasing distances from the tree. Only small seasonal fluctuations were observed, but in winter (January) there was only a significant increase in density closest (10 cm distance) to the tree. Around *Pinus* the population den-
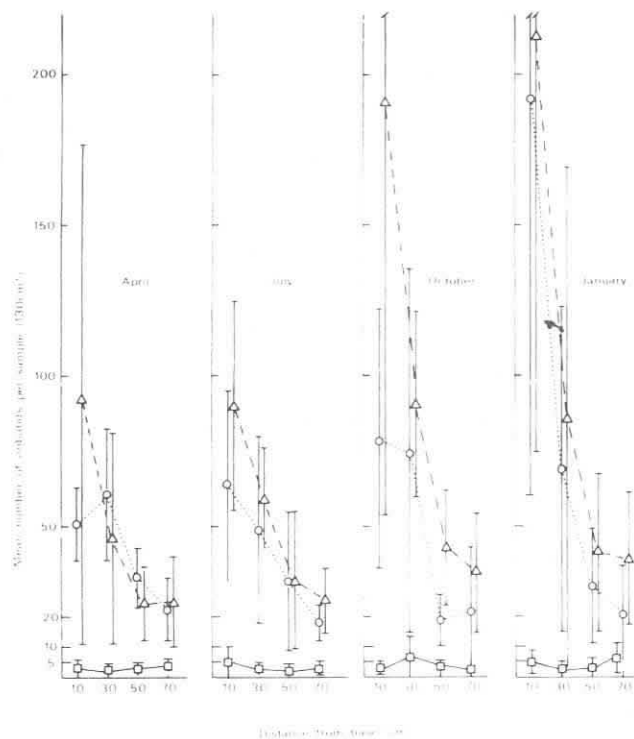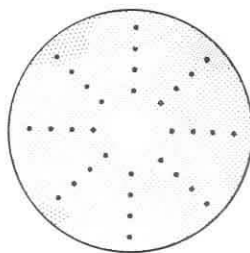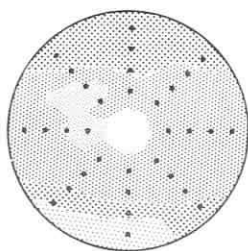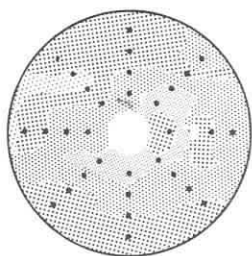

Fig. 3. Mean (+ SD) number of oribatid mites in relation to distance from the tree base of *Quercus robur* (　　　　　), *Fagus silvatica* (······) and *Pinus silvestris* (　-----) at different seasons.
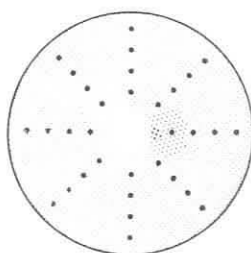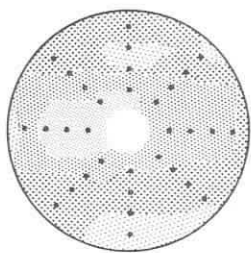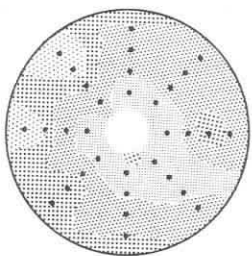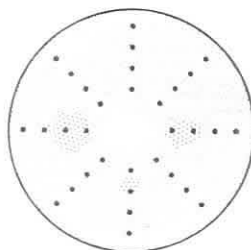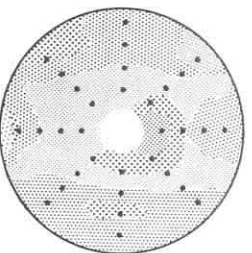
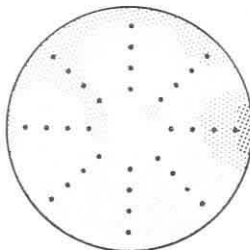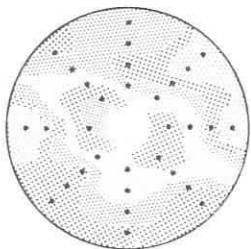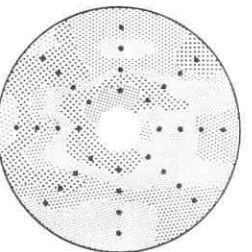P. silvestris | F. silvatica | Q. robur
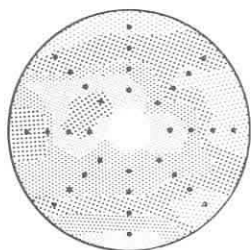
April
July
October
January

sity was higher than around *Fagus* and the gradient of decreasing density with increasing distance from the tree was steeper. The density at 30, 50, and 70 cm showed little seasonal change, but as with *Fagus* the density at 10 cm distance was much higher in winter (January) and reached over 200 individuals per 130 cm^3. Here this increase was already marked in autumn (October).

The values in Fig. 4 are based on the means of the eight samples taken on concentric circles of different radii around each tree. These means show a clear trend of decreasing population density with increasing distance from the tree base, but there are further dispersion patterns underlying these. Small scale aggregations of the oribatid populations may be responsible. The numbers of oribatids in individual samples have been used to calculate isolines of oribatid population density which were plotted as maps (Fig. 4). The overall patterns of Fig. 3 are visible but the small scale aggregations are superimposed.

Between the trees the oribatid population density was relatively low. It was similar to the area around *Quercus*, mostly between 5 and 20 individuals per 130 cm^3 and increased near to *Fagus* and *Pinus*. In the case of *Quercus* it remained at the same level (Fig. 5).

The general pattern of dispersion between and around the trees was therefore of low abundance around *Quercus*, remaining low towards *Fagus* but increasing to a very high number close to *Fagus*. Towards *Pinus* the population density first declined to a lower level and increased sharply close to *Pinus*. Subsequently it decreased again towards *Quercus*. This pattern is representative of the total oribatid population. It is made up by species with a high abundance, as for instance *Tectocepheus relatus*, for which a similar pattern was observed (SCHENKER 1983). Several species are relatively rare and do not influence this pattern. They tend to exhibit a random distribution as a result of their scarcity (SCHENKER & STREIT 1981). However, several species show a different distribution to the above, e.g. *Platynothrus peltifer* and *Brachychthonius berlesei* (Fig. 6). *B. berlesei* was not found around *Quercus*, was most abundant around *Fagus* and seldom occurred between the trees. Its population density was highest in winter (January) and decreased with increasing distance from *Fagus*, but this was reversed around *Pinus* (Fig. 6).

P. peltifer occurred in similar population densities around *Quercus* and *Pinus*, where it became more abundant with distance from the trees. Between the trees its population density remained at about this level (ca. 0–10 individuals per 130 cm^3), and only around *Fagus* was *P. peltifer* more abundant (Fig. 6). This species achieved its highest population density in spring (April).

Fig. 4. Horizontal distribution of oribatid mites from the base to ca. 1 m distance of three species of tree at different seasons. Area between isolines: (1) 1–2, (2) 2–6, (3) 6–14, (4) 14–30, (5) 30–62, (6) 62–126, (7) 126–254 and (8) 254–510 individuals per 130 cm^2. ● sample points.
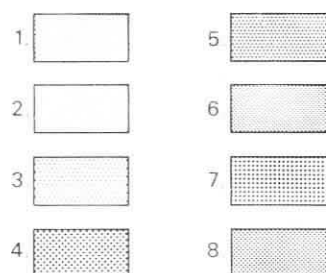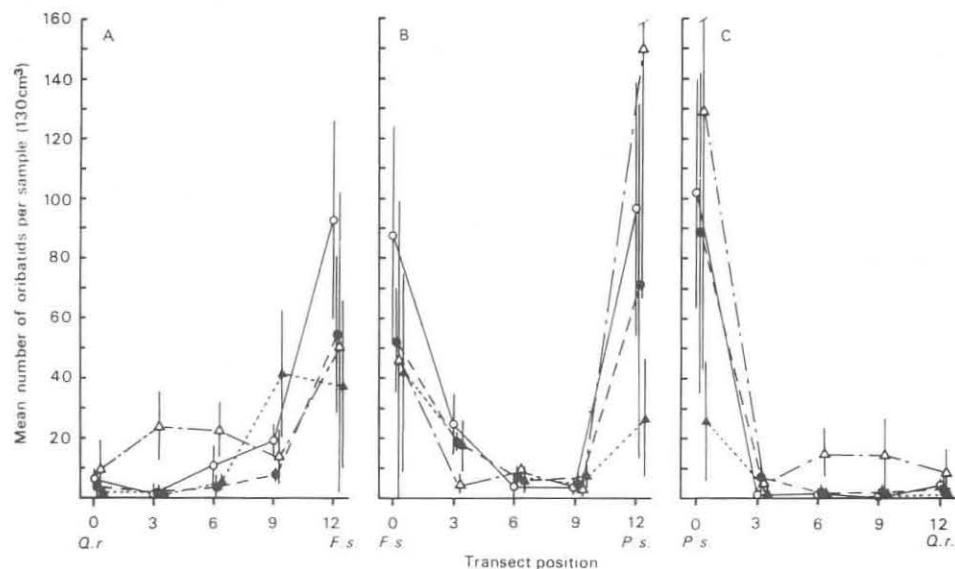
Fig. 5. Mean (± SD) number of oribatid mites on transects between trees and at different seasons
(○———○ March, ●------● June, △—·—△ September, ▲------▲ December). Distance in
meters. Positions near the trees in 30 cm distance from the base.

4.2.2. Vertical distribution

In the 20 cm depth samples taken at 30 cm distance from the trees the number of spe-
cies decreased from a total of 37 in the top 5 cm to 16, 13 and 10 in the three deeper layers
from 5 to 20 cm respectively. The total number of individuals in these samples decreased
from 2,109 in the 0—5 cm layer to 713, 501 and 350 in the three deeper layers. This shows
clearly that the largest proportion of the oribatids occurred in the uppermost 5 cm of the
soil profile, which here corresponded to the A_B-horizon. PANDE & BERTHET (1975) using
a soil sectioning technique found oribatids most abundant in the upper 3 cm of a woodland
soil. Various species behave differently, however, and different reasons have been suggested
in the literature.

In the present study the decrease of oribatid abundance with increasing depth is small near
Quercus which is a result of the overall lower population density. Near *Fagus* and *Pinus*,
on the other hand, this decrease was clearly marked except in November near *Fagus*, when
all layers had a similar abundance, i.e. the abundance in the 0—5 cm layer decreased
whereas in the deeper layers it increased (Fig. 7).

The vertical population density is plotted as isolines based on the numbers of animals in
individual samples in Fig. 8. It shows that the density decrease is not as absolute as it
seemed considering only the mean values. There were also aggregations of oribatids in the
deeper layers of the soil.

Large species were found almost exclusively in the upper 5 cm of the soil. *P. laevigatus*
never occurred in deeper layers, whereas *P. peltifer* occasionally was found in the 5—10 cm
layer. *O. tibialis*, although relatively large, was found even at 20 cm depth. On the other
hand, small species do not always occur in the deeper layers of the soil, e.g. *B. berlesei* was
found only once in samples from 15—20 cm and almost exclusively at 0—5 cm. Several
species show density patterns in relation to the tree species in the top 5 cm of soil which
correspond to the horizontal distribution patterns.

An exception to this was *O. minus* (Fig. 9), it being less abundant in the top 5 cm than
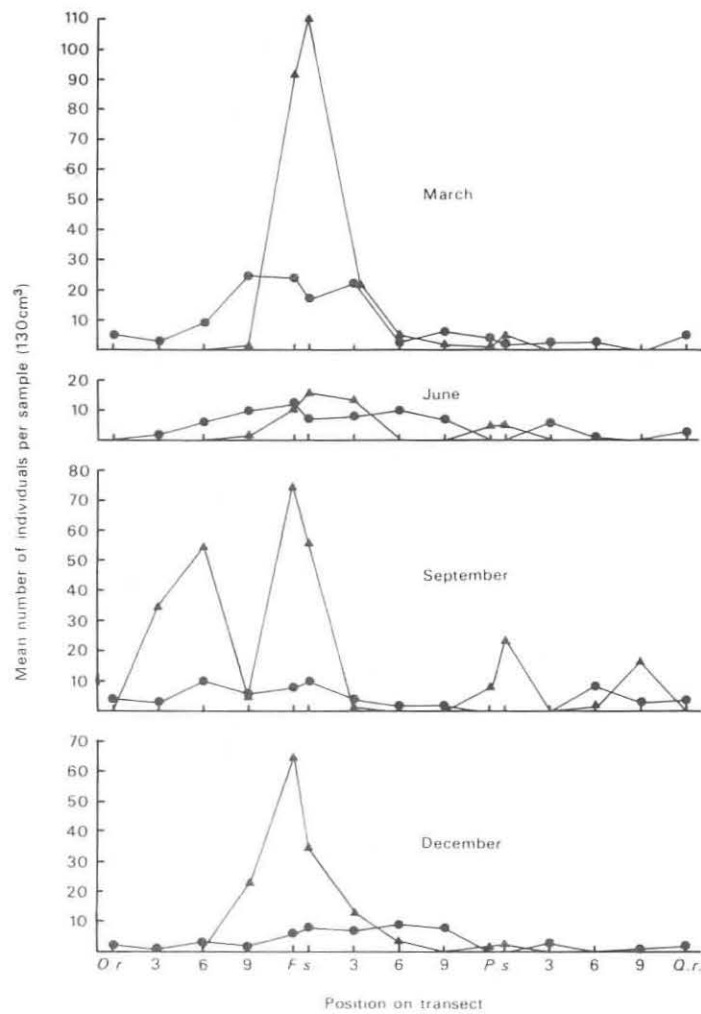in the deeper layers.

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Fig. 6. Mean number of *Brachychthonius berlesei* (▲) and *Platynothrus peltifer* (●) around the trees (30 cm distance) and on transects (distance in metres) at different seasons.

Fig. 7. Mean number of oribatid mites from 0–20 cm soil depth at 30 cm distance from *Quercus* (■), *Fagus* (●) and *Pinus* (▲) at different seasons.

Fig. 8. Vertical distribution of oribatid mites in 30 cm distance from tree bases from 0–20 cm depth and at different seasons. Area between isolines as in Fig. 4.

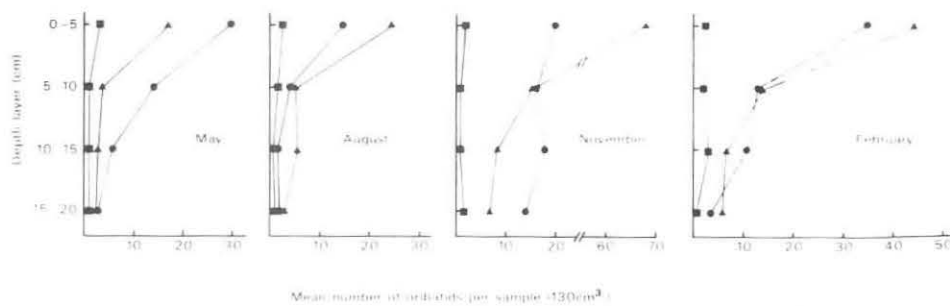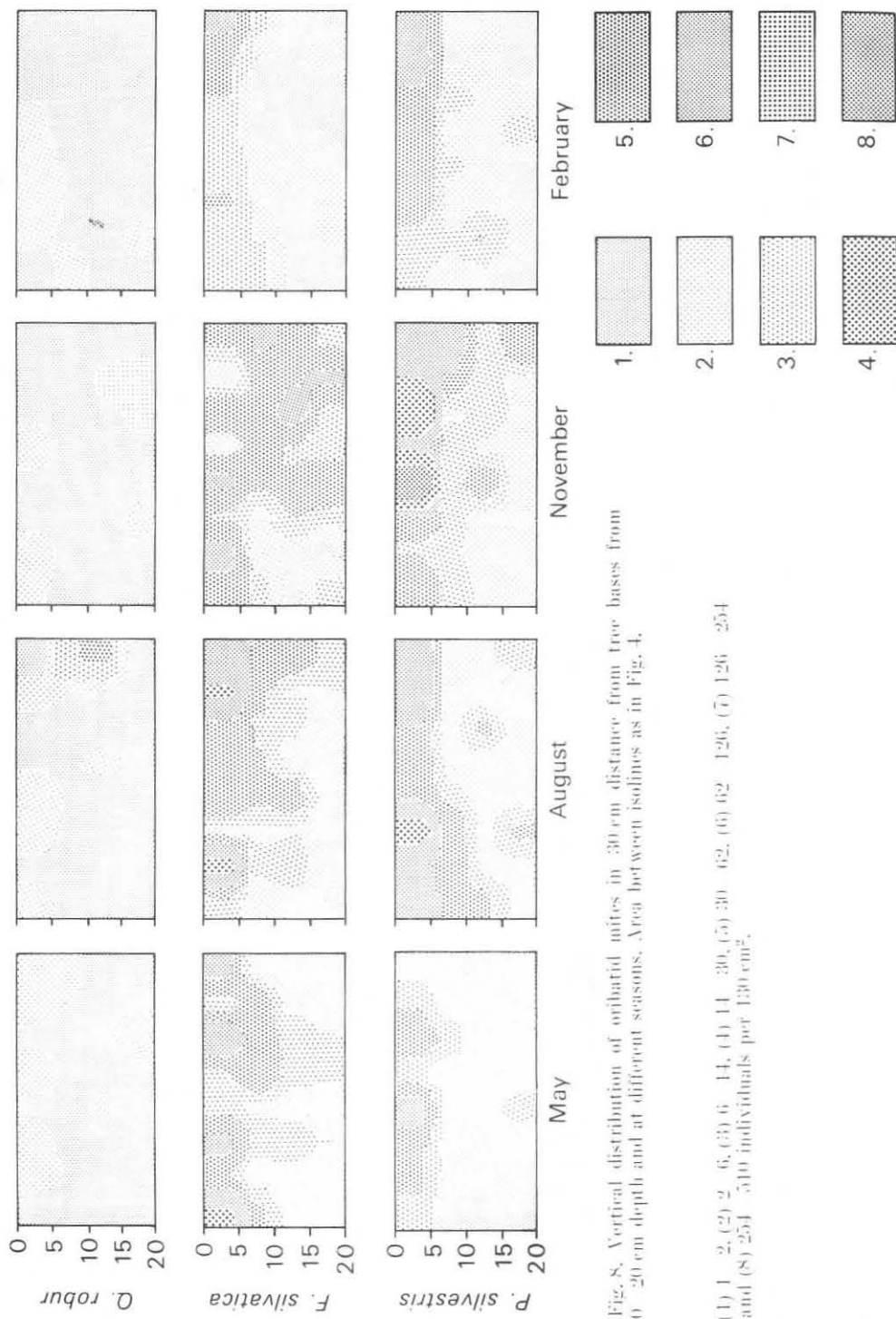(1) 1–2, (2) 2–6, (3) 6–14, (4) 14–30, (5) 30–62, (6) 62–126, (7) 126–254 and (8) 254–510 individuals per 130 cm².
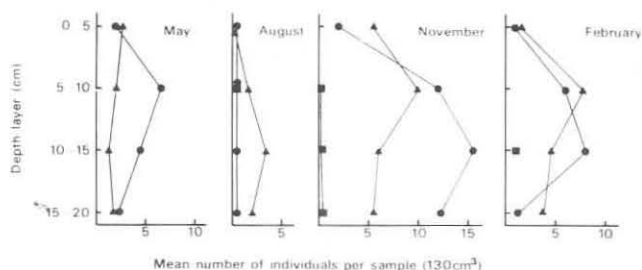
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Fig. 9. Mean number of *Oppiella minus* from 0—20 cm depth in 30 cm distance from *Quercus* (■) *Fagus* (●) and *Pinus* (▲) at different seasons.

Seasonal changes occurred in all the recorded species which were related mainly to fluctuations in the overall abundance and not to significant changes in the distribution patterns.

4.3. Biomass

The distribution of the oribatid biomass over the site corresponded partly to the density distribution. However, as large and small species were not distributed in the same ratio in the oribatid communities, there were also considerable differences in biomass and density distribution (Table 4). Compared with *Quercus* the number of individuals per m² and year around *Fagus* increased 16 times, around *Pinus* 21 times whereas the biomass increased only 3 and 4 times respectively. This was a result of the species composition around the different trees. Of the individuals around *Quercus*, large species as *P. peltifer*, *X. tegeocranus* and *S. italicus* were relatively abundant, each of these species contributed more than 10"₀ to the biomass around this tree. Around *Fagus* the adults of *P. peltifer* and *N. silvestris* contributed more than 10"₀. The small Oppiidae contributed 7"₀ because they occurred here in very high numbers, i.e. 33"₀ of all individuals. Also around *Pinus* the increase in individuals was due to small species, mainly *T. velatus*, which contributed 40"₀ of the total number of oribatids and 33"₀ of the oribatid biomass.

The seasonal changes in biomass were relatively small around *Quercus*, but marked around *Fagus* and *Pinus*. Although twice as many individuals occurred near *Pinus*, for instance, in January compared to April, the biomass decreased at the same time. This was caused by a high abundance of *T. velatus*, Suctobelbidae, Brachychthoniidae and Oppiidae in January, whereas large species were less abundant then.

Between the trees the biomass as well as the number of individuals was much lower than close to the trees, and did not change significantly when expressed as an annual mean over the whole study site. Seasonal changes were small.

With increasing soil depth both biomass and number of individuals decreased rapidly. However, the biomass decreased more rapidly because large species mainly occurred in the top 5 cm of the soil whereas small species, mainly *O. minus*, remained in greater numbers in the deeper layers of the soil profile.

4.4. Ecological parameters

Table 5 summarizes the abiotic conditions around the three trees investigated, indicating properties of the different micro-habitats. Most parameters showed small scale changes from 10 to 70 cm distance from the tree bases, either increasing as Ca around *Pinus*, pH around *Fagus* and *Pinus*, and K around *Pinus* or decreasing as pore volume, water content and C N ratio around *Pinus* and pH and carbon around *Quercus*. Most parameters however had irregular patterns around the trees. This indicates also, as for the oribatid distribution, a small scale mosaic for the distribution of the ecological parameters and therefore

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Table 4. Biomass (live mass) and number of individuals (all stages) expressed per m² as annual and seasonal means around the trees, on the transects between the trees and in different soil depth layers (a.m.: annual mean)

	Quercus		Transect		Fagus		Transect		Pinus		Transect	
	mg m⁻²	ind m⁻²	mg m⁻²	ind m⁻²	mg m⁻²	ind m⁻²	mg m⁻²	ind m⁻²	mg m⁻²	ind m⁻²	mg m⁻²	ind m⁻²
Annual mean	65.4	1,619	37.0	2,812	206.4	25,432	41.5	2,157	231.0	34,679	39.6	1,135
April March	54.5	1,435	50.5	2,012	146.5	20,654	35.3	2,574	202.8	28,057	31.3	343
July June	41.7	1,344	26.3	1,108	142.4	18,361	43.2	2,402	256.6	23,774	67.4	967
October September	67.6	1,685	41.4	4,274	168.4	24,102	37.7	1,170	277.3	44,678	42.4	2,701
January December	88.8	1,810	39.7	3,838	170.7	38,610	49.6	2,480	187.5	47,206	17.2	468
5–10 cm layer (a.m.)	1.5	152			2.6	1,436			2.4	1,135		
10–15 cm layer (a.m.)	0.2	140			1.2	1,100			1.2	710		
15–20 cm layer (a.m.)	0.2	121			1.2	686			0.9	545		

Table 5. Mean values ($\pm$ SD) of the measured ecological parameters around the three investigated tree species

	Quercus	Fagus	Pinus
Water content (%, m/m)	38.6 $\pm$ 6.5	35.8 $\pm$ 5.1	33.5 $\pm$ 4.4
Pore volume (%)	54.5 $\pm$ 5.9	53.6 $\pm$ 6.5	47.1 $\pm$ 5.4
pH	5.0 $\pm$ 0.3	4.2 $\pm$ 0.3	3.9 $\pm$ 0.3
Organic matter content (%)	5.0 $\pm$ 1.3	5.7 $\pm$ 1.6	5.2 $\pm$ 1.5
C (%)	2.3 $\pm$ 0.7	4.3 $\pm$ 2.7	2.4 $\pm$ 1.0
N (%)	0.24 $\pm$ 0.05	0.22 $\pm$ 0.22	0.18 $\pm$ 0.05
C/N	9.8 $\pm$ 3.1	11.2 $\pm$ 2.3	13.8 $\pm$ 5.7
Ca (ppm)	2,826 $\pm$ 749	593 $\pm$ 366	331 $\pm$ 177
K (ppm)	4,107 $\pm$ 801	2,198 $\pm$ 431	2,381 $\pm$ 763
Na (ppm)	2,429 $\pm$ 722	3,867 $\pm$ 641	2,645 $\pm$ 1,112

of the micro-habitats. The same is true for the transect areas although generally organic matter content, pore volume, carbon and nitrogen content as well as nutrient content was lower there than close to the trees.

Vertically organic matter content, pore volume, carbon, nitrogen, calcium, potassium and natrium content decreased rapidly in the profile.

5. Discussion

Some of the most species-rich communities in nature are found in soil systems. Well developed temperate woodland soils may contain up to a thousand species of soil animals alone, including several hundred species of mites and Collembola, in populations exceeding one to two million individuals per m² (ANDERSON 1975). How these communities are distributed, organized and how they function remains unclear (STREIT 1982). This paper has described the distribution of oribatid mites in a complex forest soil ecosystem as a basis for further ecological investigations. At the study site, around and between the three species characteristic of a Querco-carpinetum association with planted pine trees, 65 species were found. Their communities and composition differed considerably over small distances with concomitant changes in diversity. Even at one location the diversity may change temporally because the number of species in monthly samples varied. Over the site a clear pattern of distribution was described, which did not change throughout one year.

The oribatids exhibited a lower population density around Quercus (mean at 30 cm distance was 1,732 ind. m⁻²), a higher population density around Fagus (26,035 ind. m⁻²) and an even higher population density around Pinus (35,061 ind. m⁻²). Between the trees total numbers declined to a low level, which was similar to that around Quercus. The density was usually maximal closest to the tree (10 cm) and decreased rapidly in a steep gradient within 1 m (Fig. 3). Underlying this pattern were smaller aggregations (Fig. 4). These distribution patterns, although related to the habitat structure, the tree species, should not be correlated to these as such but to the specific soil, humus, root system etc. around and between them. These abiotic factors varied between the trees, e.g. the mean organic matter content was highest (6%) around Fagus, whereas around Pinus and Quercus the mean was 5% (Table 5).

However, although the distribution of these factors could be described and the different microhabitats could be characterized and related descriptively to oribatid species distribution, statistically significant correlations were difficult to detect. A non-parametric correlation analysis (SCHENKER 1981) between individual samples from the same micro-site for mite extractions and soil analysis showed a significant correlation only between total oribatid distribution and organic matter content (Kendall Rank Correlation Coefficient 0.2216; Spearman Rank Correlation Coefficient 0.3004; P < 0.025). No other factor was significantly correlated with oribatid population density, but several factors correlated with single species density. However, these correlations could be functionally more indirect,

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primarily with fungi, bacteria and algae, and thus with the food resources of most oribatid species.

POOLE (1964) showed the opposite trend of distribution in relation to tree bases for Collembola in coniferous woodlands, and suggested the number of active mycorrhizal roots as a cause.

The seasonal fluctuations in oribatid numbers affected the level of abundance, but not the structure of the distribution patterns. Seasonal changes were most marked close to the trees (*Fagus* and *Pinus*), where the numbers of oribatids increased significantly in winter. The vertical distribution pattern showed no such seasonal shifts. This suggests that seasonal migration into deeper layers did not occur, but there may have been migration of some species towards the tree base in winter.

Although the distribution patterns were relatively stable over the study year, an investigation carried out three years later (June 1982) at the same site with similar sample distribution showed some changes (GLASSTETTER 1982). Similar patterns in June 1979 and June 1982 were evident in *P. laevigatus* and *O. nova*, although their aggregation centres had moved slightly. Larger changes occurred in *P. peltifer* and *Suctobelba* spp., their area of highest population density had moved from between *Pinus/Fagus* to between *Fagus/Quercus* and showed a more even distribution. An overall decrease in population density compared to 1979 was observed for *B. berlesei*, *T. velatus*, *Suctobelba* spp. and *O. tibialis*.

It is suggested that aggregations and density gradients of oribatid populations are not purely arbitrary, but are correlated to habitat structure. Abiotic factors may affect the food resources of such oribatids and the availability of suitable micro-habitats may control their distribution. Large aggregations of oribatids with diameters of up to several metres appear to be underlain with sub-aggregations of single species, which could reflect niche separation. It remains to determine if long-term changes in these patterns occur and how they are organized and regulated.

6. Conclusions

During the course of this study 65 oribatid species were recorded. The distribution of the oribatid populations shows clear patterns in relation to the habitat structure of the heterogeneous forest soil site which was investigated. Aggregations of up to several metres in diameter with the tree trunks as centres are formed. They are underlain by smaller, mainly single species, aggregations. The aggregations may be stable over one year, but changes may occur over longer periods. Seasonal changes in distribution patterns are small, and suggest a movement of the oribatids towards the tree bases in winter rather than into deeper layers of the soil.

7. Zusammenfassung

Räumliche und saisonale Verteilungsmuster von Oribatiden (Acari: Oribatei) in einem Waldboden-Ökosystem

Von Februar 1979 bis Februar 1980 wurden monatliche Bodenproben in der Nähe und zwischen Bäumen dreier Arten entnommen. Diese drei Baumarten waren für den untersuchten Standort (eine Querco-carpinatum Assoziation mit eingepflanzten Föhren) charakteristisch. Insgesamt wurden 65 Oribatiden-Arten gefunden. Ihre Besatzdichte war am größten nahe *Pinus* (35061 Ind. m $^{-2}$), am niedrigsten nahe *Quercus* (1732 Ind. m $^{-2}$) und mittel nahe *Fagus* (26025 Ind. m $^{-2}$). Zwischen den Bäumen war die Dichte niedrig (etwa gleich wie nahe *Quercus*). Diesem Verteilungsmuster waren kleinere Aggregationen einzelner Arten unterlagert. Das allgemeine Muster veränderte sich kaum während des Untersuchungsjahres, obwohl saisonale Dichteschwankungen auftraten. Die höchste Diversität wurde um *Quercus* (E 0.5), die niedrigste um *Pinus* (E 0.3) und eine mittlere Diversität um *Fagus* (E 0.4) gefunden. Die Verteilung einzelner, in relativ geringer Anzahl auftretender Arten, war zum Teil stark verschieden vom allgemeinen Verteilungsmuster der Oribatiden, das von der Verteilung weniger häufiger Arten überprägt wurde.

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Schenker, R., 1984. Spatial and seasonal distribution patterns of oribatid mites (Acari: Oribatei) in a forest soil ecosystem. Pedobiologia **27**, 133—149.

From February 1979 to February 1980 monthly soil samples were taken around and between three tree species characteristic of the study site, a Querco-carpinetum association with planted pine trees. A total of 65 species of oribatid mites was recorded. Their density was highest around *Pinus* (35,061 ind m^{-2}), lowest around *Quercus* (1,732 ind m^{-2}) and intermediate around *Fagus* (26,025 ind m^{-2}). Density between trees was low (similar to the density around *Quercus*). This distribution pattern was underlain by smaller, single species aggregations. It did not change over one year, although seasonal density changes occurred. Diversity was highest around *Quercus* (E = 0.5), lowest around *Pinus* (E = 0.3) and intermediate around *Fagus* (E = 0.4). Distribution of single species occurring in comparatively small numbers sometimes differed significantly from the general distribution pattern which was made up of few but abundant species.

Key words: Acari, Oribatei, mites distribution patterns, biomass, diversity, species composition forest, soil.